

Disease and Insect Resistance in Cultivated Barley Accessions from the USDA National Small Grains Collection

J. Michael Bonman,* Harold E. Bockelman, Lee F. Jackson, and Brian J. Steffenson

ABSTRACT

Cultivated barley (*Hordeum vulgare* subsp. *vulgare* L.) accessions from the USDA-ARS National Small Grains Collection (NSGC) have been tested systematically for the past 20 yr for disease and insect resistance. In this study, we analyzed the resistance to barley yellow dwarf (BYD), spot blotch (SB) caused by *Cochliobolus sativus* (Ito and Kuribayashi) Drechs. ex Dastur, net blotch (NB) caused by *Pyrenophora teres* f. *teres* Drechs., stripe rust (SR) caused by *Puccinia striiformis* Westend. f. sp. *hordei*, and Russian wheat aphid (RWA), *Diuraphis noxia* (Mordvilko), with respect to (i) geographic origin of resistant accessions, (ii) relationship to other NSGC descriptor data, and (iii) relationships among resistances. "Centers of concentration" for certain resistances were identified: eastern Africa for several diseases, western Turkey and the Caucasus for SR resistance, eastern Asia for adult plant resistance to NB, and south-central Asia for RWA resistance. Stripe rust resistance was also associated with accessions originating from high altitude in eastern Africa (Ethiopia). Various associations between resistances and grain descriptors, plant habit, and landrace status were also found. Forty-eight accessions showed multiple resistances on the basis of the field disease data and the RWA greenhouse data. Many of these resistant accessions were from Ethiopia, and many were of unknown origin. Stripe rust testing in California and Bolivia supported the conclusion that winter-habit accessions were more resistant to the disease than were spring-habit accessions. Information from this study will be used to guide future NSGC acquisition and evaluation efforts.

THE NSGC CONTAINS more than 25 000 accessions of cultivated barley that have been acquired during the past 100 yr by scientists from the USDA and others interested in crop germplasm conservation and utilization. National Small Grain Collection accessions continue to be acquired, maintained, and distributed as part of an effort to assure the availability of diverse germplasm for use in developing productive, high-quality barley cultivars. Upon request, accessions from the NSGC are provided free of cost to scientists worldwide. Passport and evaluation data are found on the USDA-ARS Germplasm Resources Information Network (GRIN) at www.ars-grin.gov/npgs. Systematic gathering of descriptor data for the collection began in 1983, including evaluation of cultivated barley accessions for various agronomic, spike, seed, and quality traits as well as for resistance to important diseases and insects. Expanding the characteriza-

tion database for the barley accessions is vital to increasing the utility of the collection in choosing parents for germplasm enhancement, in genetic diversity assessments, and as baseline data for genomic research efforts.

Barley is grown worldwide across a wide diversity of environments. It is more broadly adapted than any other cereal crop and is produced in many areas that are unfavorable for production of other cereals (Poehlman, 1985). The NSGC has barley accessions from more than 90 countries, representing landraces, originally developed by farmers and collected from either farmer fields or markets, and lines and cultivars developed by plant scientists through hybridization. Few studies have been made to relate disease and insect resistance in cultivated barley accessions to geographic origin and agronomic characteristics. The limited information available indicates that disease resistance can vary depending on geographic origin and can be associated with various agronomic traits. For example, resistance to BYD disease was frequent in accessions from high elevation regions in Ethiopia (Schaller et al., 1963) and resistance was associated with various agronomic traits (Qualset, 1975).

Disease and insect resistances are critical traits for the stability and sustainability of barley production. Barley yellow dwarf is the most widely distributed and damaging virus disease of barley worldwide (D'Arcy, 1997). The disease is caused by a group of luteoviruses that are aphid-transmitted and yield losses under natural infection are estimated at about 15%. Resistant cultivars are the best control measure for BYD. Net blotch is one of the most widely distributed foliar diseases of barley. It is most severe in temperate regions of high rainfall and humidity, although epidemics have occurred in the low rainfall areas of western Australia. Many countries have reported an increased incidence of NB in the last several decades, caused in part by the more common practice of growing barley continuously in one field and with increased use of irrigation. Minimum tillage practices, which increase crop residue, also may contribute to an increase in NB because more inoculum is retained in the field. Yield losses due to NB can approach 100% in severely affected fields of highly susceptible cultivars, but more typical losses range from 10 to 40% (Steffenson, 1997). Net blotch can also reduce the quality of the grain as both kernel plumpness and malt extract yield can be diminished in barley infected with the pathogen. Spot blotch is found in nearly every region where barley is grown. However, it appears to cause significant losses only in areas with a warm, humid climate and is rarely a problem in barley grown under semiarid conditions. Spot blotch has been especially damaging in the upper Midwest region of the USA and in the central provinces of Canada. The severity of SB infection on barley can vary greatly from year to year because the pathogen is

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sensitive to environmental conditions. Yield reductions as high as 37% have been reported for susceptible cultivars in Canada. Stripe rust of barley occurs in many of the world's barley producing areas and, after being discovered in the USA in 1991 (Marshall and Sutton, 1995), it has emerged as the most important barley disease in the western USA (Line, 2002). Many races of the pathogen have been identified and host resistance is the most commonly used control measure. Russian wheat aphid is "a devastating pest on barley" (Mornhinweg et al., 1991) that is estimated to have caused more than \$1 billion in losses in the western USA since its introduction into the country in the 1980s (Bregitzer et al., 2003). Resistance from NSGC accessions has been recently incorporated into improved barley germplasm (Bregitzer et al., 2003).

During the past 20 yr, many of the NSGC barley accessions have been evaluated for resistance to BYD, NB, SB, and SR diseases and for resistance to RWA, but there has been no comprehensive analysis of these data. The purpose of this work was to analyze the NSGC data for resistance to the four diseases and RWA to elucidate relationships between resistance and other traits, including geographic origin and agronomic information available in the GRIN database, and to generate information to guide future barley acquisition and evaluation efforts.

MATERIALS AND METHODS

Disease and RWA Resistance Assessments

Accessions were tested for disease resistance across several years and locations. A total of 4719 accessions were screened in four field tests for resistance to BYD, two at Davis, CA, during 1987 and two at Urbana, IL, in 1993 and 1995. The method of Hewings et al. (1992) was used and accessions were scored on a 1-to-9 scale, where 1 was highly resistant and 9 highly susceptible.

In nine trials, a total of 14 099 accessions was tested for NB resistance including field trials (10 196 accessions) for adult-plant resistance conducted at Fargo, ND, in 1988–1989, at Athens, GA, in 1988, and at Langdon, ND, in 1990 through 1992 and 1996 and in greenhouse tests (3903 accessions) for seedling resistance conducted at Fargo in 1987 and 1989. Fifteen SB screening trials were done with a total of 20 210 accessions. Trials for adult plant resistance were conducted in the field at Athens in 1987 and at Fargo in 1988, 1990 through 1997, and 1999 (14 336 accessions) and for seedling resistance in greenhouse tests at Fargo in 1985 through 1987 and 1989 (5874 accessions). For the NB and SB field trials, barley accessions were planted in two adjacent rows of hill plots (8–12 seeds/hill) spaced 0.3 m apart. Spreader rows of susceptible cultivars Hector for NB and ND5883 for SB were planted around the double rows of hill plots to facilitate the spread of the pathogen in the disease nursery. The nursery was inoculated by scattering infected barley straw over the spreader rows (approximately 60 g/linear m of row) when the test entries were at early tillering, growth stage 23–24 (Zadoks et al., 1974). This inoculation was made using straw infected with isolate ND89-19 of *P. teres* and isolate ND85F of *C. sativus* from the previous season's crop. Disease severity (1-to-9 scale, where 1 was highly resistant and 9 highly susceptible) was assessed on the top three leaves of plants within a plot. Seedling resistance was assessed

using plants at the two-leaf stage as described by Bergland and Pederson (1981). None of the accessions were tested for both seedling and adult-plant resistance to NB and SB.

Stripe rust evaluations were completed under conditions of natural infection for 24 353 accessions in tests in Bolivia from 1991 to 1996 in single-row plots and inoculum spreader rows (Valasco et al., 1991). A group of 4020 accessions was also retested under natural disease pressure in fall-sown trials at Davis from 2000 through 2003. Many of these retested materials were winter habit types and the purpose of repeating the test at Davis was to ensure that the reactions observed in Bolivia would correlate to those in a temperate climate where winter types would flower normally. Single 2.4-m rows of each entry were sown in late fall. The cultivars Russell (susceptible) and Bancroft (resistant) were repeated checks throughout the nursery, while spreader rows of the California susceptible cultivar, Max, also were sown throughout the nursery. Disease severity ratings were made several times during the spring of each year (from heading through the early to mid-dough stage) as percentage of infection according to the modified Cobb scale (Peterson et al., 1948).

Russian wheat aphid resistance for 24 800 accessions was evaluated at Stillwater, OK, from 1995 through 2003 in a seedling-stage greenhouse test (Webster et al., 1991).

Agronomic Descriptor Data

Agronomic descriptors have been systematically recorded for the NSGC accessions. Growth habit was scored based on spring plantings at Aberdeen, ID. Spike-row number, hull type, caryopsis color, and lemma color were scored in the laboratory by standard rating codes. Landrace classification was based on information available in the passport data and is somewhat subjective.

Data Analysis

Accessions were tested across years and sometimes at more than one location. Disease resistance data therefore were scaled to the grand means for each disease to reduce effects of year-to-year differences in disease intensity on the percentage of resistant accessions identified. Greenhouse and field data were analyzed separately. Greenhouse trials with NB and SB measured seedling resistance, while field trials for these two diseases measured adult-plant resistance. Mean percentage resistance was calculated by assigning scores of 1 to 2 as highly resistant and >2 to 4 as moderately resistant for BYD, NB, and SB. Accessions with SR severity ratings of less than or equal to 5% and >5 to 20% were considered highly resistant and moderately resistant, respectively. Russian wheat aphid scores from 1 to 3 were classified as highly resistant and scores of 4 to 6 were classified as moderately resistant. Cut-off values were chosen so that, when possible, the percentage of accessions designated as highly resistant was less than 10% of the total sample tested. Because very few accessions showed RWA resistance and 86% had scores of 9 on the 1-to-9 scale, data for this trait were not scaled to the grand means. Non-overlap of the 95% binomial confidence intervals was used as a basis for determining significant differences between various groups of accessions (e.g., between accessions from different geographic regions).

Countries of origin were classified into regions on the basis of the United Nations designations for World Macroregions (United Nations, 2000). Individual barley accessions were placed on maps by one of the following methods on the basis of the level of detail available in the passport data: (i) collector notes indicating latitude and longitude, based on maps or GPS

instruments; (ii) gazetteers from the GONet Names Server (National Geospatial-Intelligence Agency, 2004) or the Getty Thesaurus of Geographic Names On Line (J. Paul Getty Trust, 2000) when the collection site was named; (iii) ArcView 8.2 (ESRI, 2002) software was used when collector notes indicated distance and direction from a city or village or other landmark; and (iv) when neither specific locality nor latitude–longitude data were available, the accessions were mapped either to state or province level or to country level only. Elevation data were derived from either collector notes indicating elevation or the GTOPO30 dataset on the Global GIS Global Coverage DVD developed by the U.S. Geological Survey and the American Geological Society (Hearn et al., 2003).

Not all disease resistance data and data for other descriptors were available for each accession, so associations between traits were assessed on subpopulations where data for both traits were available. Fisher's Exact Test was used to ascertain if there was a relationship between pairs of variables (Langsrud, 2004).

RESULTS AND DISCUSSION

Relationship to Geographic Origin

Ward (1962) used the phrase “centers of concentration” to describe the “concentration of certain characters among strains from certain regions.” Because resistance of accessions varied with geographic origin, we applied Ward's concept to the geographic distribution of disease and insect resistance of NSGC barley accessions. Clearly eastern Africa is a center of concentration for BYD resistance (Table 1). Data on BYD resistance were available for 4719 accessions, and the percentage of highly resistant accessions was greater for the sample from eastern Africa (most coming from Ethiopia), than for the total sample. This result agrees with that of Schaller et al. (1963), who screened 6689 accessions and found that 116 of 117 BYD-resistant accessions were either from Ethiopia or were derived from hybridization with Ethiopian materials. The BYD resistance in most of the Ethiopian lines studied by Schaller was due to a single dominant gene, *Yd2* (Rasmusson and Schaller, 1959). In the present study, accessions from northern America and eastern Asia showed a higher proportion ($P = 0.01$) of moderate resistance than the total sample, and the northern American accessions also showed more highly resistant accessions ($P = 0.01$) than Eastern and Western Europe accessions. The 21 highly resistant northern American accessions were all breeding lines or cultivars and, according to the GRIN database, four of the lines were developed from hybridization with Ethiopian material, seven were derived from a composite cross generated by H.V. Harlan in the 1920s that contained a diversity of germplasm including Ethiopian lines, and 10 were of unknown pedigree. Thus, some of the BYD resistance in the northern American accessions can be traced directly to Ethiopian origin and others may have Ethiopian germplasm in their pedigree. Paltridge et al. (1998) identified a molecular marker, YLM, which they used to identify lines with *Yd2*. Perhaps this marker would be a convenient tool for verifying if *Yd2* is present in the resistant accessions from northern America.

Adult-plant resistance to SB was most common in ac-

Table 1. Percentage of highly resistant (HR)[†] and moderately resistant (MR)[‡] and number of cultivated barley accessions tested (n) from the NSGC classified by geographic region.

Geographic region	BYD			SB (adult plant)			SB (seedling)			NB (adult plant)			NB (seedling)			SR			RWA		
	HR	MR	n	HR	MR	n	HR	MR	n	HR	MR	n	HR	MR	n	HR	MR	n	HR	MR	n
Eastern Africa	3.2*	19.1	507	0.1	8.5	2147	4.5*	18.4*	1115	0.5	50.6*	1494	40.9*	14.6*	759	23.0*	37.7*	4212	0.02	0.12	4239
Eastern Asia	0.2	29.6*	426	0.5	12.8*	1455	0.3	2.6	623	10.8*	38.5	1311	7.7	4.3	47	5.2	12.8	3026	0.16	0.19	3128
Eastern Europe	0.0	13.3	512	0.1	5.9	966	0.3	3.0	366	3.5	35.4	710	17.1	0.6	323	4.4	19.6	1451	0	0.5	1589
North Africa	0.6	3.6	329	0.0	6.2	533	0.0	1.1	178	1.5	42.9	324	23.5	35.3*	17	3.1	11.3	736	0.13	3.36*	744
North America	1.6	26.3*	1295	1.7*	15.9*	2839	0.2	5.1	631	2.5	31.5	2257	19.7	2.0	254	2.1	8.2	3771	0.13	1.14	3858
North Europe	0.4	3.3	275	0.3	7.4	758	0.3	2.0	296	1.5	53.5*	613	7.0	4.6	282	7.0	23.0*	1233	0.16	0.56	1245
South America	0.7	8.2	134	0.0	5.2	967	0.0	0.0	51	1.1	50.2*	271	11.1	3.8	26	2.7	8.5	1139	0	0.17	1145
South-Central Asia	0.2	10.1	436	0.2	7.1	1295	1.2	8.0	262	3.4	37.1	626	7.9	5.4	128	3.0	5.6	2430	0.92*	2.13*	2392
Southern Europe	0.0	16.9	130	0.2	3.3	823	0.4	6.4	252	0.5	54.9*	627	4.5	17.2*	198	8.6	22.4	1233	0	0	1245
Unknown	–	–	0	0.0	2.5	204	–	–	0	8.1*	51.4*	185	9.1	0.0	22	27.1*	23.7	207	0	0	207
Western Asia	0.0	15.3	203	0.0	3.9	1040	0.4	7.4	941	3.0	33.3	663	6.8	7.0	744	10.1*	25.1*	2266	0.13	0.6	2341
Western Europe	0.0	9.8	408	0.1	6.2	1002	0.1	7.4	1053	1.7	52.1*	843	8.3	6.5	1006	5.3	17.7	2189	0	0.18	2210
Total Sample§	0.9	17.2	4719	0.5	8.7	14336	1.1	7.8	5874	3.2	41.8	10197	15.9	7.7	3862	8.3	18.5	24353	0.16	0.73	24800

[†] Highly resistant for SB, NB, and BYD = scores 1–2; for RWA = scores 1–3; for SR = severity 0–5%.

[‡] Moderately resistant for SB, NB, and BYD = scores > 2–4; for RWA = scores 4–6; for SR = severity > 5–20%.

[§] Total includes some accessions classified into regions other than those listed.

* Significantly greater than the total sample value based on non-overlap of the 95% binomial confidence intervals.

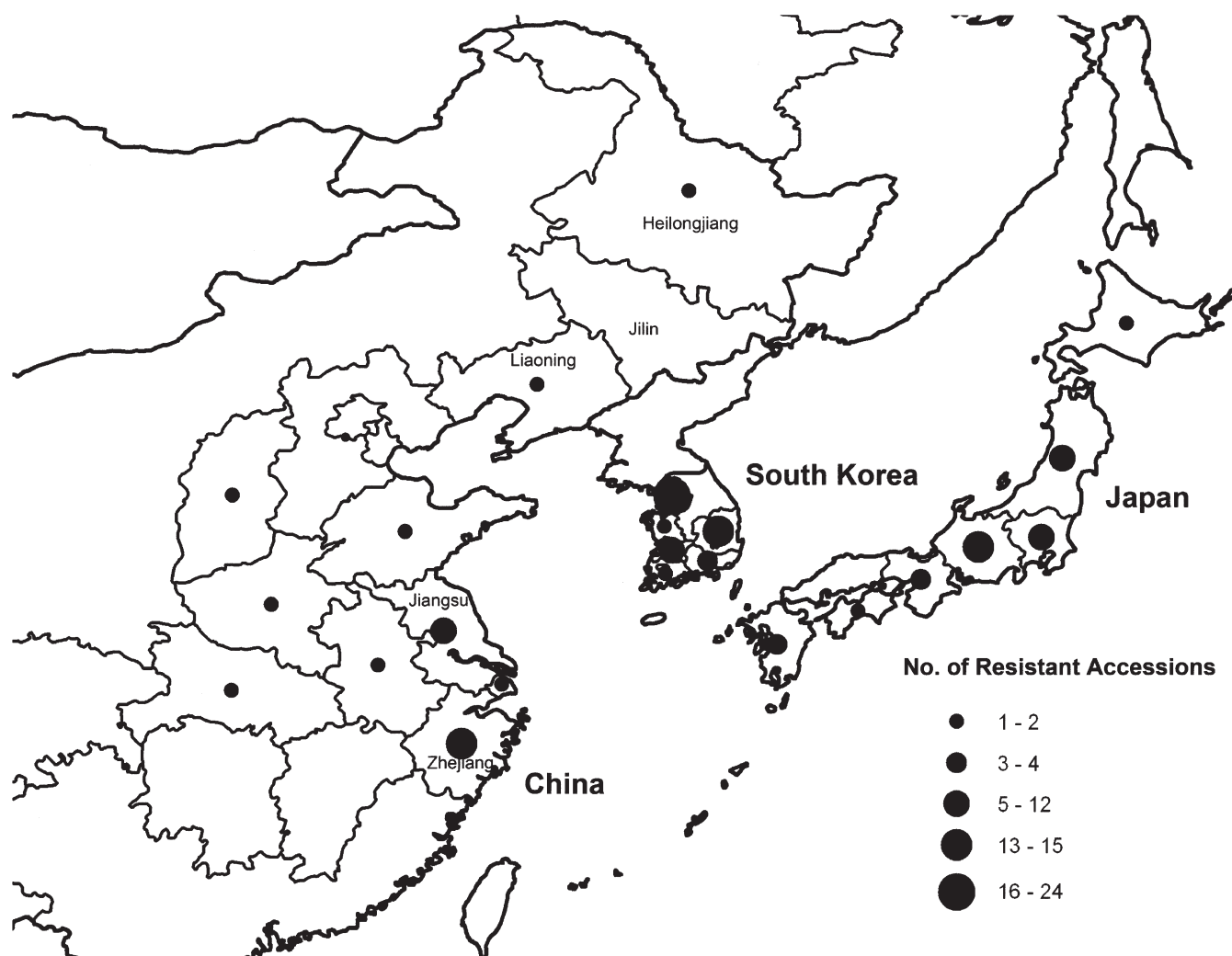


Fig. 1. Number of NSGC cultivated barley accessions highly resistant to net blotch as adult plants mapped to province of origin in China, South Korea, and Japan.

cessions from northern America ($P = 0.01$), for both highly resistant and moderately resistant accessions (Table 1). However, the greenhouse seedling trials revealed a different geographic pattern of resistance, with moderate and highly resistant accessions being most common among eastern Africa accessions ($P = 0.01$). The northern American accessions with adult plant SB resistance were primarily breeding lines, perhaps indicating selection by breeders in North America for resistance to this disease in the field. Out of the total of 66 resistant accessions identified, eight were from the USA. Based on the pedigree information available, the SB resistance of these accessions probably derives from CI 7117-77, a selection from composite cross CC-XIII (Wilcoxson et al., 1990) generated by G.A. Wiebe in the 1940s. Most of the resistant accessions were from Canada and 38 of these 39 resistant accessions were donated by C.A. St-Pierre of Laval University, Quebec. The resistance of these lines probably originated from USA germplasm via western Canada (C.A. St-Pierre, personal communication). Pedigree information supports this hypothesis. For example, nine sister lines designated QB 710 all showed resistance to SB. One of the parents of these lines

was UM 68-340, which in turn has the line CI 7117-77 in its parentage. In addition to these northern America sources of SB resistance, moderate adult-plant SB resistance was also found in eastern Asia.

Adult-plant NB resistance was most common in accessions from eastern Asia (Table 1). Most of the 1311 eastern Asia accessions for which NB field data were available originated from three countries: China (715), South Korea (263), and Japan (241). The occurrence of highly resistant accessions was much higher ($P = 0.01$) in South Korea (25.1%) and Japan (13.7%) compared with China (5.6%). Within China, a clear geographic pattern of resistance was evident with the highest proportion of resistance from the central coastal provinces of Zhejiang (15 of 44) and Jiangsu (10 of 26) and a low proportion from the northeastern provinces of Liaoning, Heilongjiang, and Jilin (3 of 297) (Fig. 1). Thus, the central coast of China, South Korea, and Japan represent a center of concentration for adult plant resistance to NB.

As with SB, the pattern for NB seedling resistance differed from that of adult-plant resistance. Accessions from eastern Africa showed the highest frequency of

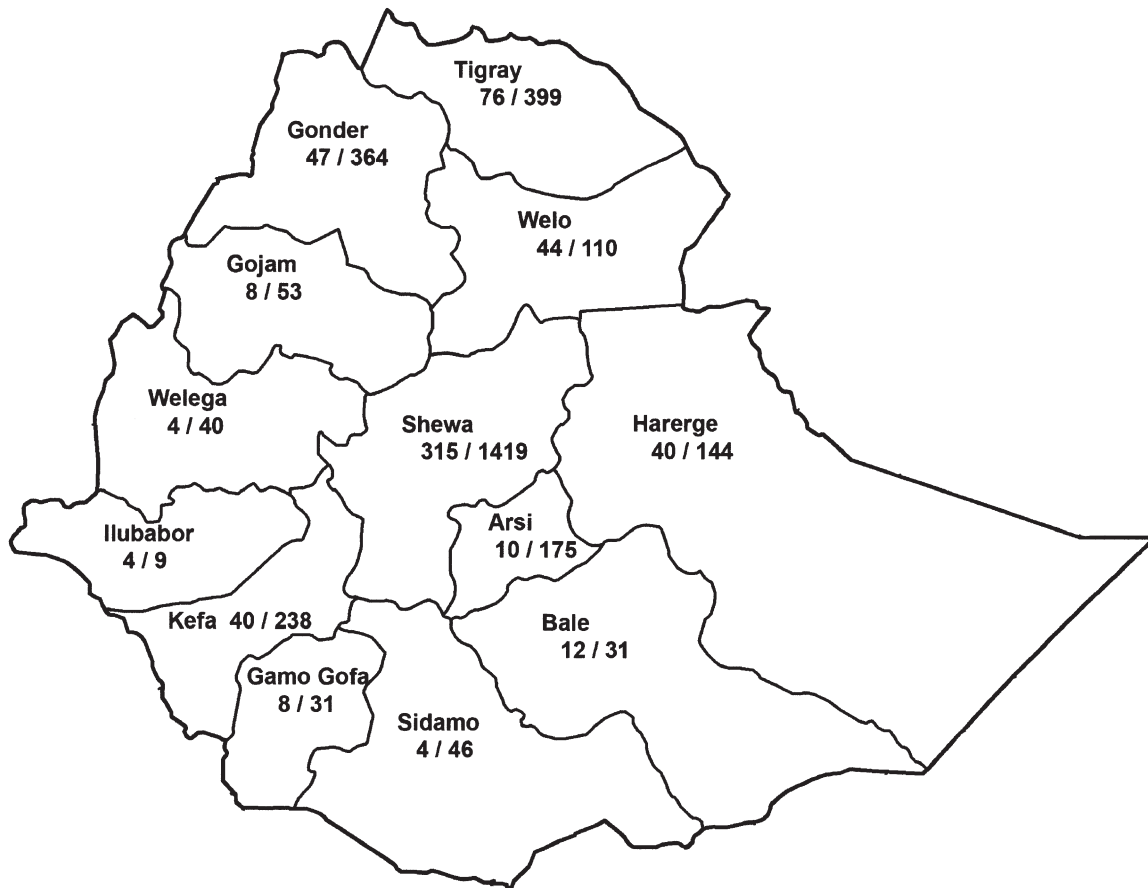


Fig. 2. Number of NSGC cultivated barley accessions highly resistant to stripe rust (numerator) and total collected (denominator) mapped to province of origin in Ethiopia.

highly resistant accessions at the seedling stage ($P = 0.01$).

Stripe rust resistance was most frequent among accessions from eastern Africa (primarily Ethiopia) and western Asia, and among accessions of unknown origin (Table 1). Ethiopia had the highest total number of SR resistant accessions (964 or 48% of the resistant accessions identified) of any country or region and is a center of concentration for SR resistance. Resistant accessions were found in every province in Ethiopia with no clear in-country geographical focus for the occurrence of resistance (Fig. 2). Within the countries of western Asia, accessions highly resistant to SR were frequent in collections from Azerbaijan (18.3%, $n = 93$), Iraq (13.8%, $n = 65$), Georgia (11.1%, $n = 108$), and Turkey (10.0%, $n = 1764$). Although Iraq and Georgia border Turkey and Azerbaijan borders Georgia and Turkey, it appears that the occurrence of resistant accessions is not localized in this contiguous border region (Fig. 3). The resistant accessions from Iraq originated from the central part of the country and, moreover, resistance within Turkey is clearly concentrated in the western part of the country and not in the eastern part bordering Georgia and Azerbaijan (Fig. 3). Thus, there could be three geographic foci for SR resistance in the western Asia region: western Turkey, central Iraq, and the Caucasus region. The center of concentration in western Turkey is supported by (i) the large number of accessions tested and

(ii) the significant differences in resistance ($P = 0.01$) between eastern and western Turkey. Western Turkey (west of Ankara and Konya provinces) had 15.8% highly resistant accessions and 32.3% moderately resistant accessions ($n = 767$), whereas eastern Turkey had 3.4% highly resistant and 14.1% moderately resistant accessions ($n = 686$). The center of concentration in Iraq is not as certain because only 65 accessions from this country were evaluated in total. Azerbaijan, Georgia, and the southwest Russian Federation are part of the Caucasus region. The southwest Russian Federation collectively showed 6.8% highly resistant and 42.1% moderately resistant accessions compared with 4.1 and 13.8% for accessions of non-Caucasus origin within the Russian Federation. Armenia is part of the Caucasus, but only 34 accessions were tested from this country. Although none of the accessions from Armenia were highly SR resistant, nine showed moderate SR resistance. These data from the Caucasus support the hypothesis that the region represents a center of concentration for SR resistance.

Resistance to RWA was rare in NSGC cultivated barleys. Nearly all accessions were tested for RWA resistance ($n = 24\,800$) and only 39 accessions (0.16%) were highly resistant and 181 accessions (0.73%) were moderately resistant (Table 1). There was a clear center of concentration for RWA resistance in South-central Asia (Table 1). Within South-central Asia, nearly all of the

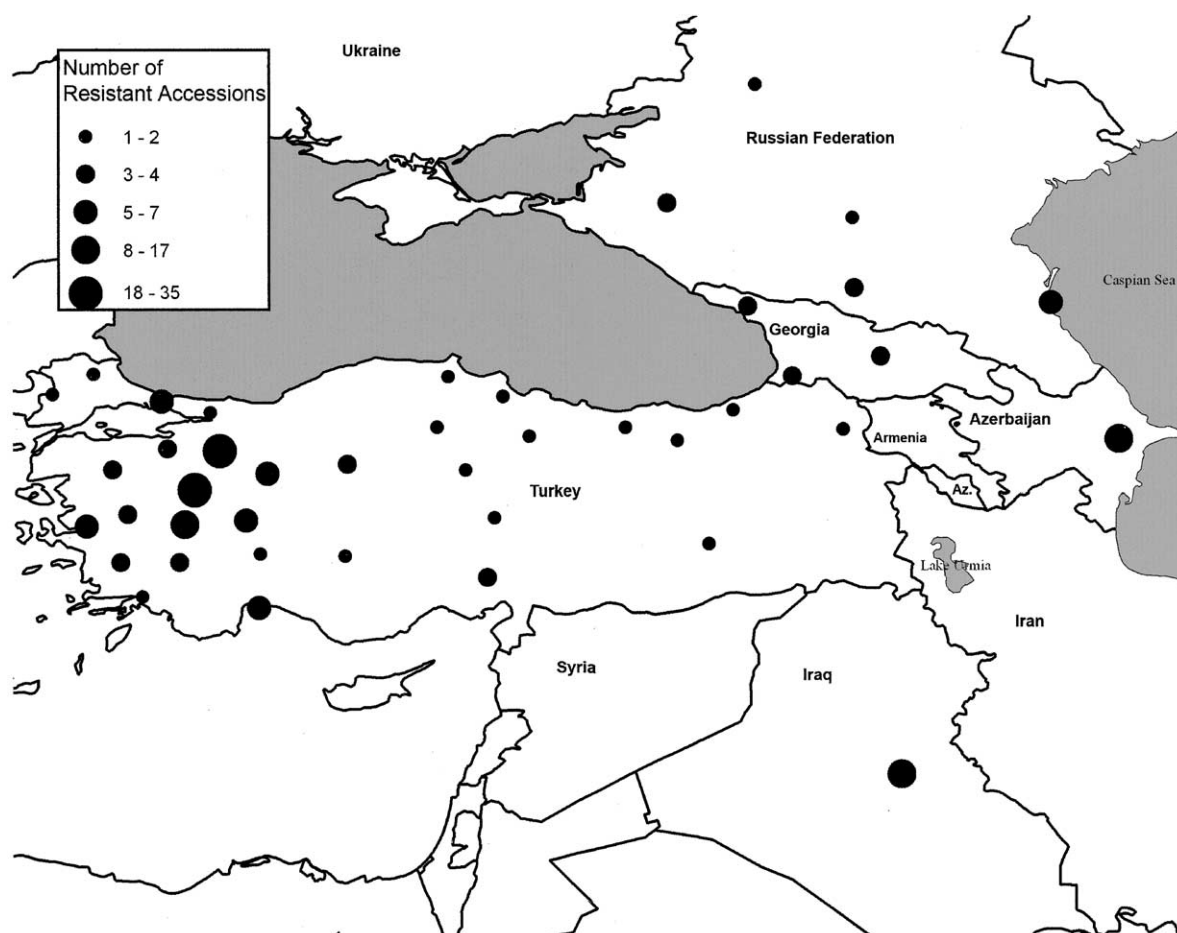


Fig. 3. Number of NSGC cultivated barley accessions highly resistant to stripe rust mapped to province in Turkey and the Caucasus region.

resistant accessions originated from either Afghanistan (3.3%, $n = 397$) or Iran (2.1%, $n = 326$). The resistant and moderately resistant accessions map not only to the border region between the two countries but also to western Iran and eastern Afghanistan (Fig. 4). A few moderately resistant accessions map to neighboring Iraq and Pakistan.

Northern Afghanistan and Iran could be considered part of the region described as the native range of the RWA, “the area between the Caucasus Mountains and the Tian Shan” mountains (Halbert and Stoetzel, 1998). This area would also presumably include Turkmenistan, Uzbekistan, Tajikistan, and Kyrgyzstan and southern Kazakhstan. Only 98 accessions from these five countries are found in the NSGC; 97 were tested and none were resistant to RWA. Given the geographic proximity of these countries to Iran and Afghanistan, and their inclusion in the native range of the pest, further collection there might yield more RWA-resistant barleys.

For Ethiopian barleys, Qualset (1975) found a gradient of increasing frequency of BYD resistance with increasing elevation of accession origin from less than 2135 m to greater than 3660 m. For the NSGC the elevation of origin values were established for 2836 of the accessions from Ethiopia and of these only 268 accessions had been tested for BYD resistance and only two were resistant. Thus, for this small sample, it was not pos-

sible to establish a trend with elevation for BYD resistance. Similarly, for most of the other diseases, either the number of tested or the number of resistant accessions were too low to show significant trends corresponding to elevation. For SR, however, disease resistance and elevation data were available for 2820 Ethiopian accessions. The accessions were divided into groups by increments of increasing elevation so that each increment contained at least 500 accessions. No gradient of increasing resistance was evident, but the highest increment of elevation, from 2732 to 3508 m, did show a significantly greater incidence ($P = 0.01$) of highly resistant accessions (31.5%) compared with lower elevations (18.0%).

When considering all elevation and disease resistance data available across regions, there was a significant relationship between elevation and SR resistance, but this relationship disappeared when the values from Ethiopia were excluded. The only other significant relationship between resistance and elevation across regions was for NB seedling resistance. Accessions collected from above 2135 m showed a significantly ($P = 0.01$) higher frequency of highly resistant accessions (32.3%, $n = 362$) versus accessions from lower elevations (11.5%, $n = 1314$). However, there were few non-Ethiopian barleys from high elevation in the total dataset, and this relationship again disappeared when the Ethiopian acces-

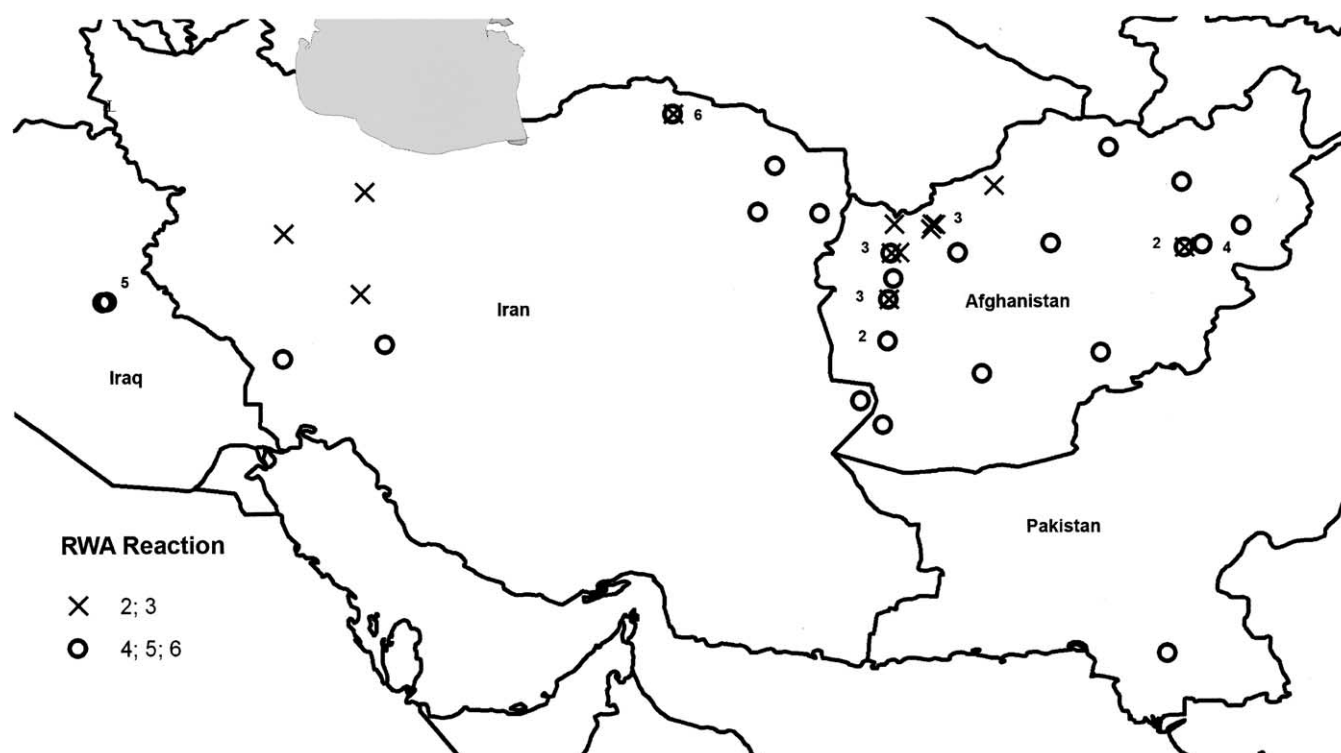


Fig. 4. NSGC cultivated barley accessions resistant to Russian wheat aphid mapped to original collection sites in Iraq, Iran, Afghanistan, and Pakistan. Numbers indicate accessions mapping to the same point.

sions were excluded. Thus, this apparent relationship between elevation and seedling resistance to NB may be an artifact of the Ethiopian accessions being more frequently resistant and over-representing the sample of high elevations accessions within the total dataset.

Relationship to Agronomic Descriptors

Resistance within the NSGC barley accessions was associated with various grain characters (Table 2). Stripe

rust and NB seedling resistances showed the most associations with aleurone and lemma color and RWA resistance showed no associations with these descriptors (Table 2). Stripe rust and NB seedling resistances were associated with aleurone and lemma color probably because these resistances were common among eastern African accessions. In this region, accessions frequently have colored lemma and aleurone (Ward, 1962). For example, in the present study, eastern African acces-

Table 2. Association between resistance to various barley diseases and selected descriptors for accessions in the NSGC.†

Descriptor	BYD	SB (adult plant)	SB (seedling)	NB (adult plant)	NB (seedling)	SR	RWA
Aleurone, Black	ns	ns	ns	ns	+ (10 ⁻¹⁴)	+ (10 ⁻²⁷)	ns
Aleurone, Black and Brown	ns	ns	ns	ns	ns	+ (10 ⁻⁴)	ns
Aleurone, Blue	ns	ns	ns	ns	+ (10 ⁻⁵)	+ (0.002)	ns
Aleurone, Grey	ns	ns	ns	ns	+ (0.03)	+ (0.003)	ns
Aleurone, Purple	ns	ns	ns	ns	+ (10 ⁻⁹)	+ (10 ⁻⁴)	ns
Aleurone, White/amber	ns	ns	ns	ns	- (10 ⁻¹³)	- (10 ⁻³⁰)	ns
Aleurone, Yellow	ns	ns	ns	ns	ns	ns	ns
Lemma, Black	ns	ns	ns	ns	+ (10 ⁻⁸)	+ (10 ⁻¹³)	ns
Lemma, Grey	ns	ns	+ (0.05)	ns	+ (0.03)	+ (10 ⁻¹¹)	ns
Lemma, Purple	ns	ns	ns	ns	+ (10 ⁻⁹)	+ (10 ⁻¹¹)	ns
Lemma, White/amber	+ (10 ⁻⁴)	+ (10 ⁻⁶)	ns	+ (10 ⁻¹¹)	- (10 ⁻²⁸)	- (10 ⁻¹¹)	ns
Lemma, Yellow	- (10 ⁻⁴)	- (10 ⁻⁵)	ns	- (10 ⁻¹⁰)	ns	ns	ns
Winter habit	- (10 ⁻⁸)	ns	+ (10 ⁻²⁰)	+ (10 ⁻⁵⁶)	+ (0.009)	+ (10 ⁻⁶)	+ (0.03)
Two-row spike	ns	ns	+ (10 ⁻⁴)	- (0.006)	- (10 ⁻²⁴)	ns	- (0.03)
Hulled	ns	+ (0.07)	ns	- (0.03)	- (10 ⁻⁵)	- (0.02)	+ (0.01)
Landrace	ns	- (10 ⁻⁸)	+ (10 ⁻⁷)	+ (0.03)	+ (10 ⁻⁵)	+ (10 ⁻⁸⁸)	+ (0.02)
BYD	-	ns	ns	ns	ns	+ (10 ⁻⁵)	ns
SB (field)	-	-	nd‡	ns	ns	ns	ns
SB (greenhouse)	-	-	-	ns	ns	+ (0.003)	ns
NB (field)	-	-	-	-	nd‡	ns	ns
NB (greenhouse)	-	-	-	-	-	+ (10 ⁻¹²)	ns
SR	-	-	-	-	-	-	ns

† Numbers in parenthesis are probability of independence of the two variables based on Fisher's Exact Test.

‡ nd = no determination possible because no accessions were tested for both characteristics.

sions represented less than 20% of the sample for which aleurone and lemma color were available but represented 70% of the accessions with black aleurone and 78% of the accessions with black lemma. For SR, only the associations with white/amber lemma and aleurone, black and brown aleurone, and blue aleurone were present if eastern Africa accessions were excluded from the analysis. For NB seedling assays, only associations with white/amber lemma and aleurone, purple lemma and aleurone, and black aleurone were present if eastern Africa accessions were excluded from the analysis. Qualset (1975) found BYD resistance among Ethiopian accessions was associated with “white and purple grain color,” whereas no association was found for purple aleurone in the present study, possibly because of the smaller sample size available. Barley yellow dwarf resistance was associated with white/amber lemma, similar to Qualset’s result, and disassociated with yellow lemma. The same relationship was present for SB and NB adult-plant resistance. Thus, the present study extends the results of the previous work with BYD to include SB, NB, and SR diseases and RWA.

There was a strong association between winter habit and adult-plant resistance to NB (Table 2), and the mean incidence of resistance across all accessions tested was significantly higher ($P = 0.01$) for winter habit (8.9%, $n = 2318$) compared with spring habit (1.4%, $n = 7625$). As discussed previously, many of these resistant accessions were from eastern Asia, with China showing a lower overall occurrence of resistance than either South Korea or Japan. However, of 131 winter habit accessions from China, 27.5% had adult-plant resistance to NB, similar to the incidence of resistance among winter barleys from South Korea (33.7%, $n = 172$) and Japan (22.3%, $n = 130$). A low frequency of resistance occurred among accessions classified as spring habit. The fact that adult plant NB resistance predominated among winter habit accessions raises the possibility that these accessions may not have been adequately vernalized under the field test conditions and that the extended vegetative growth stage in turn might have affected the resistance assessment. However, for at least the Langdon trials since 1991, it is certain that only accessions that were fully vernalized were considered. Many of the accessions that showed resistance in those trials were winter habit accessions from eastern Asia. In addition, winter barleys from regions other than eastern Asia were tested in most years and these showed a lower ($P = 0.01$) incidence of resistance (4.2%, $n = 1863$) than did those from eastern Asia (28.1%, $n = 455$). These data support the conclusion that eastern Asia winter accessions have a high degree of NB adult plant resistance. However, given the possibility of uncontrolled variables across years and locations, further NB testing with these accessions is warranted.

Relationship among Resistances

A total of 48 accessions showed multiple resistances based on the field data and the RWA greenhouse data

(Table 3). Stripe rust resistance was present in all but one of the accessions with multiple resistances; because nearly all accessions were tested for SR resistance (Table 1), the incidence of SR was relatively high (8.3%), and SR resistance was associated with BYD resistance (Table 2). Accessions from eastern Africa were the most common among the multiple resistant accessions, and, as with BYD resistance, resistance from other regions can sometimes be traced by pedigree analysis back to Ethiopian germplasm. For example, the origin of accession CIho 2230 is listed in the NSGC database as northern America (Table 3). This material was the product of a cross made in 1920 at Aberdeen, ID, between two Ethiopian barleys. Similarly, CIho 1295 was from a cross between Moravian and Deficiens. Deficiens is likely synonymous with CIho 2325, a selection from an Ethiopian landrace with multiple resistances (Table 3).

Accessions of unknown origin are greatly overrepresented in the multiple resistances group. These accessions make up less than 1% of the accessions in the total sample yet accounted for more than 20% of the accessions with multiple resistances. According to NSGC records, the accessions of unknown origin were obtained from a N.I. Vavilov nursery growing at Kharkov, Ukraine, in 1930. The Vavilov nursery likely contained accessions originating in countries where he had collected extensively before 1930, including the Mediterranean, western Asia, and Ethiopia (Vavilov, 1997). The multiple resistances of these accessions indicate a possible origin of Ethiopia. Further effort is needed to characterize these accessions via morphological characters and molecular markers so that their relationship to accessions of known origin might be established.

For NB and SB diseases, genes for resistance at the seedling stage can differ from those conferring resistance at the adult-plant stage (Steffenson et al., 1996) and for SB the seedling test does not predict adult-plant reactions (Nutter and Pederson, 1984). Furthermore, the present analysis shows that the seedling and adult-plant data differ in several characteristics, such as associations with agronomic descriptors, associations with other resistances, and geographic origin of resistant accessions. Thus, future evaluations of accessions should be performed under both field and greenhouse conditions. Data for both seedling and adult resistance across a broad range of accessions would enable a more comprehensive understanding of the relationship of these resistances to one another.

More than 4000 accessions that had been evaluated for SR resistance in Bolivia were re-tested at Davis, CA. Of these materials, 2994 were classified as winter types, 747 were classified as spring types, and the rest were classified as either facultative or mixed types. It was hypothesized that winter accessions tested under short-day conditions in the tropics might show higher resistance than under temperate conditions, thus biasing the tests in Bolivia. However, of the winter accessions tested, 3.4% were resistant at both test sites, 7.1% were resistant in Bolivia and susceptible at Davis, 12.3% were susceptible in Bolivia and resistant at Davis, and 77.3% were susceptible at both sites. Since more of the winter

Table 3. Barley accessions from the NSGC with multiple resistances.†

ACP	ACNO	Name	Status	Habit	BYD	NB	SB	SR	RWA	State	Country	Region
PI	21378	Malster	cultivar	facultative	–	2	8	1	9	New South Wales	Australia	Australia and New Zealand
CIho	938	Abyssinian	landrace	spring	1	6	8	1	8	–	Ethiopia	Eastern Africa
CIho	1223	Abyssinian	landrace	spring	2	1	7	1	9	–	Ethiopia	Eastern Africa
CIho	1225	Abyssinian	landrace	spring	1	5	8	1	9	–	Ethiopia	Eastern Africa
CIho	1230	Abyssinian	landrace	winter	–	1	4	0	9	–	Ethiopia	Eastern Africa
CIho	1236	Abyssinian	breeding	spring	1	5	8	1	9	–	Ethiopia	Eastern Africa
CIho	1240	Abyssinian	landrace	spring	1	6	8	1	9	–	Ethiopia	Eastern Africa
CIho	1604	Hillsa	landrace	spring	2	5	8	1	9	–	Ethiopia	Eastern Africa
CIho	2325	Deficiens	landrace	spring	1	5	7	1	9	–	Ethiopia	Eastern Africa
CIho	2376	Abyssinian	landrace	spring	2	5	7	1	9	–	Ethiopia	Eastern Africa
CIho	4373	–	landrace	spring	7	2	8	1	8	–	Ethiopia	Eastern Africa
CIho	5020	–	breeding	spring	2	2	6	1	9	–	Ethiopia	Eastern Africa
PI	195965	9741	landrace	spring	–	6	1	1	8	Welo	Ethiopia	Eastern Africa
PI	195967	9743	landrace	spring	–	5	1	1	9	Welo	Ethiopia	Eastern Africa
PI	382308	GAW 78-2	landrace	spring	–	1	4	1	9	Tigre	Ethiopia	Eastern Africa
PI	386814	IAR/B/503-2	landrace	winter	–	–	–	0	2	Tigre	Ethiopia	Eastern Africa
CIho	2470	Tambis	landrace	winter	–	1	6	1	9	Zhejiang	China	Eastern Asia
PI	39498	Kaosein	landrace	winter	–	1	5	1	9	Jiangsu	China	Eastern Asia
PI	39506	Wansnipe	landrace	winter	–	2	–	1	9	Zhejiang	China	Eastern Asia
PI	39519	Koran	landrace	winter	–	1	3	1	9	Shanghai	China	Eastern Asia
PI	39525	Chukiang	landrace	winter	–	1	8	1	9	Zhejiang	China	Eastern Asia
PI	190724	Bozu Omugi	landrace	winter	4	2	5	1	9	Hokkaido	Japan	Eastern Asia
PI	76502	3953	landrace	winter	–	1	–	1	8	Dagestan	Russian Federation	Eastern Europe
PI	76503	3955	landrace	winter	–	2	–	0	8	Dagestan	Russian Federation	Eastern Europe
PI	327819	WIR 13999	landrace	winter	5	2	6	1	9	Dagestan	Russian Federation	Eastern Europe
CIho	1128	Albacete	breeding	spring	2	3	7	5	9	Minnesota	United States	North America
CIho	1295	Redfield	breeding	spring	1	9	8	5	9	Minnesota	United States	North America
CIho	2230	–	breeding	spring	1	7	7	1	9	Idaho	United States	North America
CIho	1389	Abed	cultivar	spring	7	2	8	1	9	–	Denmark	Northern Europe
CIho	3832	–	landrace	winter	–	1	4	1	9	Jammu and Kashmir	India	South-Central Asia
CIho	3866	–	landrace	winter	–	2	5	0	2	Jammu and Kashmir	India	South-Central Asia
CIho	4165	Afghanistan	landrace	spring	2	4	5	90	3	Herat	Afghanistan	South-Central Asia
PI	58053	252	landrace	winter	–	1	5	1	9	Avila	Spain	Southern Europe
PI	95095	405	landrace	spring	–	2	4	1	9	–	Unknown	Unknown
PI	95098	415	landrace	spring	–	2	7	1	9	–	Unknown	Unknown
PI	95101	433	landrace	spring	–	2	7	1	8	–	Unknown	Unknown
PI	95102	439	landrace	spring	–	2	6	1	8	–	Unknown	Unknown
PI	95208	426	landrace	spring	–	2	8	1	8	–	Unknown	Unknown
PI	95244	659	landrace	spring	–	2	6	1	9	–	Unknown	Unknown
PI	95270	399a	landrace	spring	–	2	7	1	9	–	Unknown	Unknown
PI	95271	401b	landrace	spring	–	2	8	1	8	–	Unknown	Unknown
PI	95277	484	landrace	spring	–	2	7	1	9	–	Unknown	Unknown
PI	95282	494	landrace	spring	–	2	6	0	9	–	Unknown	Unknown
CIho	14325	CIho 4299-2	landrace	winter	3	2	8	0	9	–	Azerbaijan	Western Asia
PI	27829	Black Russian	landrace	winter	–	1	5	1	9	–	Georgia	Western Asia
PI	178614	II-20	landrace	winter	3	2	7	0	9	–	Turkey	Western Asia
PI	178615	II-21	landrace	winter	5	2	8	1	9	Istanbul	Turkey	Western Asia
PI	315939	Mamie	cultivar	spring	5	2	7	1	9	Nord	France	Western Europe

† Based on field disease resistance tests and greenhouse RWA tests; BYD, NB, SB, RWA scored on 1–9 scale, SR severity scored 1–100%; ACP = accession prefix, ACNO = accession number, – = no data available.

types were susceptible in Bolivia versus Davis ($P = 0.01$), there was no indication that testing winter types in Bolivia was biasing the results toward greater resistance. Furthermore, the correlation coefficient for SR scores from both sites for winter accessions was 0.47, which was identical to the correlation coefficient for the spring accessions. For the spring accessions tested at both locations, 1.6% were resistant at both test sites, 2.6% were resistant in Bolivia and susceptible in Davis, 1.6% were susceptible in Bolivia and resistant in Davis, and 92.7% were susceptible at both sites. These data support the conclusion that winter accessions are in general more resistant to SR. The differential reactions of some accessions between Bolivia and Davis is most likely due to the presence of different races of the pathogen (Line, 2002) at each test location.

In summary, our study has identified possible directions for further work within the NSGC including (i) the need to assess both adult plant and seedling resistance to SB and NB, (ii) further verification of adult-plant NB resistance in eastern Asian winter accessions, (iii) the need to expand BYD resistance testing, and (iv) the desirability of determining the original geographic source of accessions obtained from the Vavilov nursery in the Ukraine. In addition, the information we generated through this study should be useful to breeders and pathologists by helping increase the probability of finding resistance by association with various geographic origins and agronomic descriptors. The accessions identified with multiple resistances should also be directly useful for more easily accumulating resistance in breeding lines through hybridization.

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